# DEVONIAN CHONETACEAN BRACHIOPODS FROM SOUTH AFRICA

By

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# (With 10 figures)

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#### ABSTRACT

Six species of chonetacean brachiopods are recorded from the Lower-Middle Devonian Bokkeveld Group of South Africa, with the bulk of the material coming from the Emsian-Eifelian Ceres Subgroup. *Kentronetes africanus* and *Aseptonetes capensis* are described as new species, and *Anoplia* is recorded from South Africa for the first time, extending its range within the Malvinokaffric Realm. Most specimens, except some of the larger *Notiochonetes* and *Pleurochonetes*, come from fine-grained deposits, suggesting a preference for the tranquil subtidal conditions of benthic assemblages 4 and 5. Although much less diverse, the fauna shows strong palaeobiogeographic affinities with those from South America and the Falkland Islands.

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### **INTRODUCTION**

Brachiopods usually form an important part of the marine fauna found in fossiliferous Palaeozoic rocks and, in many cases, they were the dominant elements in shallow-water benthic communities of the time. In Devonian rocks, chonetaceans often form a significant proportion of the brachiopods recovered and this is certainly true for the Bokkeveld Group of South Africa.

The fossiliferous nature of the Bokkeveld Group sediments was recognized in the early part of the nineteenth century, but few attempts at systematic descriptions of the fossil remains were made until Andrew Geddes Bain submitted a collection of specimens to the Geological Society of London in 1852. The brachiopods, described by Sharpe (1856), included nine species, two of which were assigned to *Chonetes*.

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During subsequent years, extensive mapping by the Geological Commission of the Cape of Good Hope led to the discovery of many more fossils and a representative collection was sent to England for identification. Reed (1903) described the brachiopods and increased the number of species present to 23.

The work of Ulrich (1893) in Bolivia drew attention to the close similarity between that country's Devonian fauna and others known from South America, the Falkland Islands and South Africa. As more work was carried out on the South American faunas by Thomas (1905), Knod (1908), Clarke (1913) and Kozlowski (1913, 1923), and with further collecting in South Africa, so Reed continued to revise and add to the Bokkeveld brachiopod fauna (1906, 1907).

Reed published his final revision of the Bokkeveld fauna in 1925, in which the number of brachiopod species recorded was increased to 37, including six chonetaceans. Since then little formal taxonomic work has been done on the brachiopods apart from Boucot *et al.* (1963), Boucot *et al.* (1965) and Hiller (1987). Mention has been made of particular South African forms in Cloud (1942) and Boucot & Harper (1968) but without detailed descriptions. Other references to the Bokkeveld brachiopods have come in papers dealing with palaeobiogeography and/or palaeoecology, e.g. Boucot *et al.* (1969), Boucot (1970, 1971, 1975*a*), Copper (1977) and Hiller & Theron (1988), but systematic descriptions were not included in any of these.

Reed (1925: 28) noted that many of the South African species were established on poorly preserved material and that it would have been better had specific names not been applied. He made the same comment about the South American faunas and Branisa (1965) proposed *nomima nuda* for some taxa without proper descriptions. A revision of the Bokkeveld brachiopods is therefore warranted. In light of more recent work in South America, e.g. Isaacson (1977), Racheboeuf & Branisa (1985) and Racheboeuf (1992), this paper makes a start with the chonetacean representatives in the fauna. This follows from an earlier paper (Hiller 1987), in which an attempt was made to clear up the confusion regarding the identity of those specimens that had been referred to *Chonetes falklandicus* Morris & Sharpe and *Notiochonetes*.

Specimens described are housed either in the South African Museum, Cape Town (SAM numbers) or in the Albany Museum, Grahamstown (AM numbers).

#### STRATIGRAPHIC DISTRIBUTION

The currently recognized lithostratigraphical subdivision of the Bokkeveld Group (Fig. 1) was established by Theron (1970, 1972) and revised by the South African Committee for Stratigraphy (1980). The Bokkeveld Group is the middle division of the tripartite Cape Supergroup and appears to have been deposited during a period of relative crustal instability. Lithologically the group consists of a number of predominantly argillaceous units alternating with predominantly arenaceous units to which Theron (1970) assigned formational status. The sediments are arranged into a number of coarsening-upward sequences that imply phases of tectonically controlled regressions and transgressions coupled with delta out-building and reworking (Tankard *et al.* 1982: 352). Southwards the arenaceous units die out and the most southerly outcrops appear to represent a deeper-water shelf facies.

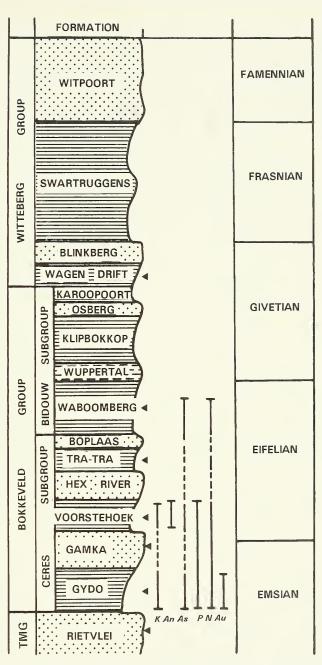


Fig. 1. Stratigraphic column of the Devonian rocks in South Africa showing the ranges of species described in this paper. Black triangles indicate the formations from which chonetid brachiopods have been recorded. *K*-Kentronetes; An-Anoplia; As-Aseptonetes; P-Pleurochonetes; N-Notiochonetes; Au-Australostrophia. Stipple shading indicates sandstone-sdominated horizons; horizontal lines indicate finer-grained units.

That the Bokkeveld Group is of Devonian age was established by the early workers, e.g. Reed (1903), but a more precise dating proved to be something of a problem. The ages of the various stratigraphic units indicated in Figure 1 are based on arguments put forward by Boucot *et al.* (1969), Theron (1970, 1972) and Boucot (1975*a*) on the basis of the marine invertebrate fossils of the Ceres Subgroup. More recently, Cooper (1986) used eustatic changes in sea-level to effect a correlation with European and North American sequences and suggested that the marine portion of the Bokkeveld Group was late Emsian-Eifelian in age.

Marine invertebrate fossils are characteristic of the lower part of the Bokkeveld Group, up to and including the fourth shale horizon, i.e. the whole of the Ceres Subgroup, plus the Waboomberg Formation (Fig. 1). However, by far the greatest number of specimens has been recovered from the Gydo and Gamka formations at the base of the group (Hiller & Theron 1988). Chonetacean brachiopods are here recorded from the lowest three formations of the Bokkeveld Group plus the Tra-Tra and Waboomberg formations. Possible chonetaceans have also been noted from the Rietvlei Formation at the top of the Table Mountain Group (Hiller & Theron 1988) and from the Wagen Drift Formation at the base of the Witteberg Group (Hiller & Dunlevey 1978).

# FAUNAL LIST OF DEVONIAN CHONETIDS FROM SOUTH AFRICA

The South African Devonian brachiopod fauna is, overall, a very conservative one, showing much lower diversity in terms of genera and species than contemporary faunas from Europe or North America. It is also apparently less diverse than equivalent South American faunas. Among the chonetaceans only six genera, each represented by a single species, are currently recognized. The equivalent fauna in Bolivia contains 20 species belonging to 11 genera of chonetaceans (Isaacson 1977; Racheboeuf & Branisa 1985; Racheboeuf 1992).

The South African Devonian chonetaceans are represented by the following taxa:

#### Family Strophochonetidae

Kentronetes africanus sp. nov. Australostrophia clarkei Racheboeuf & Herrera, 1994

#### Family Anopliidae

Subfamily Anopliinae

Anoplia cf. A. belenensis Racheboeuf & Branisa, 1985

# Family Chonetidae

Subfamily Chonetinae

Aseptonetes capensis sp. nov.

Subfamily Notiochonetinae

Notiochonetes skottsbergi (Clarke, 1913) Pleurochonetes falklandicus (Morris & Sharpe, 1846)

Apart from these, other Malvinokaffric taxa may be present in South Africa. Reed (1925) described and figured the internal mould of a pedicle valve that he identified as *Chonetes (Eodevonaria)* aff. *arcuata* Hall. However, he stated that the specimen did not show any spines or crenulations (denticles) along the hinge line, a feature diagnostic of *Eodevonaria*. Muir-Wood (1962: 93) included Reed's record in the list of species to be included in *Eodevonaria*, but Boucot & Harper (1968: 151) categorically rejected the specimen from the genus and stated that *Eodevonaria* had not been recognized in the Malvinokaffric Realm. Subsequently, Isaacson (1977) discovered a species of *Eodevonaria* in Peru and again raised the possibility (p. 174) that Reed's specimen may belong in the genus. Herrera (1991) has recorded *Eodevonaria* from Argentina and it has now been found in Bolivia (P. R. Racheboeuf pers. comm. 1994).

Reed (1925: 46) mentioned that a specimen from the southern Cape in the Sedgwick Museum, Cambridge, did show denticles along the hinge line. The author has examined two pedicle valve internal moulds labelled as *C. (Eodevonaria)* aff. *arcuata* in the Sedgwick Museum, although they were originally identified as *C. falklandicus*. One of them possessed some denticles along one-half of the hinge line but assignment to *Eodevonaria* would only be tentative at best. Therefore, unless better-preserved material is found, the presence of the genus in South Africa must be regarded as still unsubstantiated.

Other Bolivian forms, such as Austronoplia and Babinia, have not been positively identified from South African rocks but the possibility exists that, with further collecting, they may well turn up in the Bokkeveld fauna. Several small specimens that the author originally identified as Babinia lacked an enlarged median costa and hence are regarded as juveniles of Kentronetes, but Reed (1925) described Chonetes ruecki medialis as a new subspecies of C. ruecki Ulrich differing from it principally in possessing an enlarged median rib. Reed's specimen is shown here as Figure 3H. Racheboeuf & Branisa (1985) placed C. ruecki in Quadrikentron and erected Babinia for small specimens possessing an enlarged median costa and lacking a dorsal median septum. Reed's specimen (1925, pl. 4 (figs 7–8)) may well belong in Babinia, but it is not sufficiently well preserved for such an assignment to be certain.

Reed (1925: 44) transferred several small shells that he had originally (Reed 1903) identified as *Chonetes* aff. *C. setiger* Hall to *Chonetes stuebeli* Ulrich, which is now the type species for the genus *Austronoplia* Isaacson, 1977. However, Reed did not describe the interior of the brachial valve and, from his illustrations, the pedicle valve could just as well belong to *Aseptonetes*.

### PALAEOECOLOGY

The Bokkeveld Group chonetacean brachiopods show a preference for environments in which finer-grained clastic sediments were deposited. As can be seen in Figure 1, they tend to occur in those formations that are predominantly shale and mudstone, although they are occasionally found in sandier horizons within these formations. Only *Pleurochonetes* and *Notiochonetes* have been recovered from the sandstone-dominated Gamka Formation.

Hiller & Theron (1988) outlined a number of benthic communities that can be recognized within the Bokkeveld Group, which has been interpreted as a series of stacked deltaic cycles (Tankard & Barwis 1982). Chonetacean brachiopods are found in each of the depositional settings associated with the deltas, but particularly in the distributary mouth bar, delta slope, and prodelta shelf communities. *Notiochonetes* appears to have preferred the shallow-water distributary mouth bar and delta-slope environments, probably the equivalent of benthic assemblages 3 and 4 of Boucot (1975*a*). Evidently the large flattish *Australostrophia* and *Kentronetes*, and the small *Aseptonetes* and *Anoplia* preferred the deeper, less-turbulent settings of the lower delta slope and shelf as they are only known from muddy horizons, i.e. benthic assemblages 4 and 5. *Pleurochonetes* seems to have tolerated a wider range of conditions as it has been recovered from distributary mouth bar, delta slope and shelf sediments, i.e. benthic assemblages 3–5. No chonetaceans are known for certain from the tidal-flat community but, if their occurrence in the Wagen Drift Formation of the Witteberg Group can be confirmed, then they may be found in such a setting. Similarly, the possible occurrence of chonetaceans in the Rietvlei Formation at the top of the Table Mountain Group suggests their presence in a lower shoreface community (Hiller & Theron 1988: 238).

When any of the species associated with muddy environments is found in sandy horizons within the shaly units, they usually occur as dissociated valves resting in a convex-up position on a bedding surface. This may indicate some transport before relatively slow burial. In contrast, when they are found in the mudstones they often occur as complete shells, suggesting fairly rapid burial. Their orientation within the sediment is usually random, however, probably as a result of the intense bioturbation normally observed in these units (Toots 1965).

The larger, flatter forms probably lived free on the sea-floor, using their spines for stabilization in the manner suggested by Brunton (1972) and Racheboeuf (1990), but the discovery of a complete specimen of *Aseptonetes capensis* sp. nov. in close association with a plant fragment raises the question as to whether the shell was attached to the plant during life. Plant fragments are not uncommon in these shallow clastic environments and the juxtaposition of the specimens may simply be a chance occurrence, but the possibility remains that at least some small chonetaceans may have made use of suitable substrates for attachment if such were available. Racheboeuf (1990: 165) has suggested that small chonetaceans, especially those with long asymmetrical spines, probably lived epiplanktonically, attached to algae or floating organisms.

# PALAEOBIOGEOGRAPHIC AFFINITIES

The Devonian fossils of the Bokkeveld Group have long been regarded as belonging to, and typical of, the Malvinokaffric palaeobiogeographic realm (Boucot *et al.* 1969; Boucot 1988). It is not surprising, therefore, that the chonetacean brachiopods within the Bokkeveld fauna show greatest similarity with those in other parts of this realm, including the Falkland Islands, Bolivia, and the Paraná Basin of Brazil. Of the forms described here, *Australostrophia* and *Notiochonetes* are endemic to the Malvinokaffric region, having been recorded from Bolivia, Brazil, the Falklands, South Africa, and possibly Argentina and Uruguay (Boucot *et al.* 1969: 27; Melo 1988: 695). *Pleurochonetes* and *Aseptonetes* are similarly likely to be Malvinokaffric endemics. The former shows the same distribution as *Australostrophia* and *Notiochonetes*, whereas *Aseptonetes* is so far known only from Bolivia and South Africa.

The genus *Kentronetes* has recently been erected for Malvinokaffric realm strophochonetids (Racheboeuf & Herrera 1994) and is thus also endemic to the

realm. Racheboeuf & Branisa (1985) recorded it from Bolivia as *Quadrikentron*. Its occurrence in South Africa extends the geographic range of the genus within the Malvinokaffric Realm. *Anoplia* is a genus with an almost cosmopolitan distribution during Early Devonian times. It occurs in the Eastern American Realm, the Rhenish-Bohemian and Tasman regions of the Old World Realm, and the Malvinokaffric Realm (Boucot *et al.* 1969). The South African occurrence extends its range further.

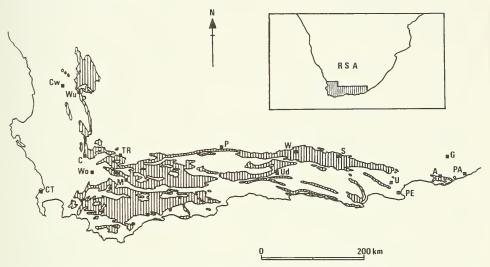


Fig. 2. Map showing the outcrop of the Bokkeveld Group rocks in the Cape Province and indicating the positions of towns mentioned in the text. A-Alexandria, C-Ceres, CT-Cape Town, Cw-Clanwilliam, G-Grahamstown, M-Montagu, P-Prince Albert, PA-Port Alfred, PE-Port Elizabeth, S-Steytlerville, TR-Touws River, U-Uitenhage, Ud-Uniondale, W-Willowmore, Wo-Worcester, Wu-Wuppertal.

# SYSTEMATIC PALAEONTOLOGY

Suborder CHONETOIDEA Muir-Wood, 1955

Superfamily CHONETACEA Bronn, 1862

### Family Strophochonetidae Muir-Wood, 1962

Genus Kentronetes Racheboeuf & Herrera, 1994

Kentronetes africanus sp. nov. Figs 3-4

Chonetes falklandicus non Morris & Sharpe, 1846. Reed, 1903: 171-172, pl. 20 (figs 9-10).

# Material and horizon

Holotype. AM 5187 in the Albany Museum, Grahamstown. Internal mould of a brachial valve from the Voorstehoek Formation, Alexandria district, eastern Cape (see Fig. 2). *Paratypes*. AM 5175-1, AM 5188-AM 5191, SAM-13400: internal and external moulds of 14 pedicle valves and 4 brachial valves from the Gydo Formation in the Wuppertal and Ceres districts of the western Cape, and 21 pedicle and 3 brachial valves from the Voorstehoek Formation in the Alexandria district of the eastern Cape.

#### Diagnosis

A species of *Kentronetes* with markedly transverse elliptical outline (length/width ratio about 0.60), three spines on either side of umbo in adult stages, and lacking any sort of median septum or ridge in the brachial valve.

#### Description

Small to medium sized (maximum length 17.6 mm) plano- to gently concavo-convex shells with transversely sub-rectangular to sub-elliptical outlines; maximum width at a little over two-fifths of valve length from umbo; cardinal extremities rounded or obtuse. Pedicle valve about three-fifths as long as wide; very gently convex in both lateral and anterior profiles. Umbo small; interarea short, flat, apsacline; delthyrium with small apical pseudodeltidium. Brachial valve interarea very short, catacline; no chilidium observed. Radial ornament of fine, low, rounded capillae that increase by branching and intercalation to number 100-120 at anterior margin, with a density of 16-19 (most commonly 17) ribs in a 5-mm sector at the 10-mm growth stage. Three small specimens show development of enlarged median costa with rounded cross-section and extending to valve margin from about one-third valve length. Two, or maximum three, spines on either side of umbo, at high angles  $(66^{\circ}-75^{\circ})$  to hinge line. Spines about 2 mm apart, nearest 5 mm from umbo.

Pedicle valve interior with small, obliquely elongate hinge teeth directed anterolaterally, without dental plates. Muscle field broadly triangular, two-thirds as long as wide and almost two-fifths as long as valve; anterior margin weakly impressed, posterior bounding ridges low, gently curved and diverging at about 100°. Median septum low, narrow, up to one-quarter as long as valve. Large triangular diductor scars enclose small, elongate, oval adductor scars.

Brachial valve interior without median septum. Bilobed cardinal process fused to proximal ends of long, widely divergent, curved inner socket ridges. Sockets moderately deep, curved. Anderidia long, very narrow, diverging at about  $55^{\circ}-60^{\circ}$ . Muscle field about four-fifths as long as wide and about one-third as long as valve, bisected by shallow median groove extending anteriorly from in front of cardinal process.

Dimensions (in mm)

Pedicle valves	length	width
AM 5175	3.5	5.6
AM 5189	13.9	28.7
AM 5190	14.4	30.5
SAM-13400	12.7	24.9

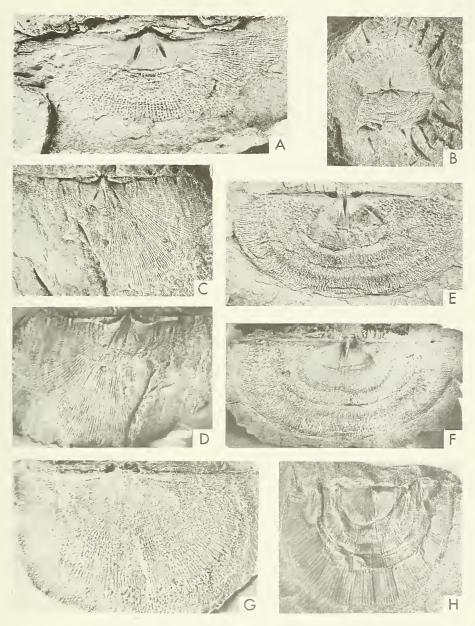


Fig. 3. A-G. Kentronetes africanus sp. nov. A. AM5187, holotype, internal mould of a brachial valve, × 2.9. B. AM5175-1, internal mould of conjoined pedicle and brachial valves, × 4.1. C-D. AM5188, internal mould and latex cast of a brachial valve, × 2.1 and 2.2, respectively. E-F. AM5190, internal mould and latex cast of a pedicle valve, × 2.1. G. AM5191, latex cast of a brachial valve exterior, × 2.1. H. Babinia? medialis. SAM-7779, external mould of a brachial valve, × 4.2 (Reed's holotype of Chonetes ruecki medialis). A and C-G are from the Voorstehoek Formation in the Alexandria district, eastern Cape; B is from the Gydo Formation, near Wuppertal, western Cape; H is probably from the Gydo Formation in the Hex River Valley.

### Discussion

The specimens described here are most similar to *Quadrikentron ruecki* (Ulrich, 1893), described from Bolivia by Racheboeuf & Branisa (1985). The main difference with the South American species is that the South African shells are slightly larger and possess a significantly more transverse outline. They also lack a dorsal median septum, even the wide low ridge seen in the Bolivian specimens. In most other respects they are very similar. *Quadrikentron ruecki* has recently been transferred to *Kentronetes* by Racheboeuf & Herrera (1994).

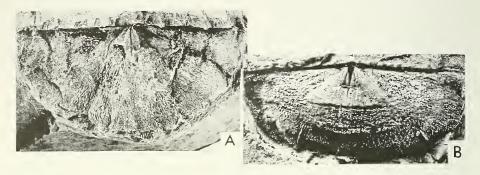


Fig. 4. Kentronetes africanus sp. nov. A. SAM-13400, internal mould of a pedicle valve, × 2.6. B. AM 5189, internal mould of a pedicle valve, × 1.9. A is probably from the Gydo Formation in the Ceres district, western Cape; B is from the Voorstehoek Formation in the Alexandria district, eastern Cape.

Genus Australostrophia Caster, 1939

### Remark

The decision to place *Australostrophia* in the family Strophochonetidae follows Racheboeuf & Herrera (1994).

# Australostrophia clarkei Rachebeouf & Herrera, 1994

Fig. 5

Stropheodonta cf. S. concinna (Morris & Sharpe). Reed, 1903: 169, pl. 22 (fig. 6). Stropheodonta (Leptostrophia) concinna (Morris & Sharpe). Reed, 1925: 41. Australostrophia clarkei Rachebeouf & Herrera, 1994: 556, fig. 5a-f.

### Material and horizon

Internal and external moulds of 9 pedicle valves and 2 brachial valves from the Gydo Formation, north of Clanwilliam in the western Cape Province (Fig. 2).

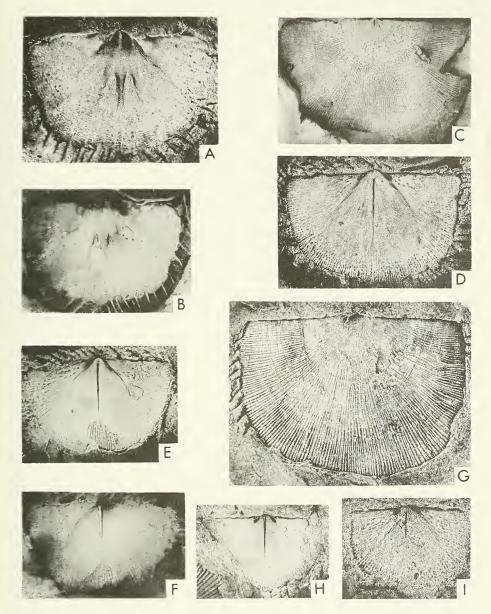


Fig. 5. Australostrophia clarkei Racheboeuf & Herrera, 1994. A-B. AM 5186-2, internal mould and latex cast of a brachial valve, × 3.1 and 2.3, respectively. C. AM 5186-5, latex cast of a pedicle valve exterior, × 1.7. D. AM 5186-1, internal mould of a pedicle valve, × 2.1. E-F. AM 5185-1, latex cast and internal mould of a pedicle valve, × 2.4. G. AM 5184, external mould of a pedicle valve, × 2.5. H. AM 5185-2, internal mould of a pedicle valve, × 2.4. I. AM 5186-3, internal mould of a pedicle valve, × 3. All from the Gydo Formation north of Clanwilliam, western Cape.

#### **Description**

Medium to large plano-convex shells with semi-circular outline, maximum width along hinge line; cardinal extremities slightly acute to slightly obtuse. Two pairs of spines situated on either side of umbo. Pedicle valve about two-thirds as long as wide; gently convex in both lateral and anterior profiles with greatest convexity in umbonal region, becoming flatter towards the posterolateral margins. Ventral interarea short, apsacline. Delthyrium closed by large convex pseudodeltidium. Brachial valve flat. Dorsal interarea very short; anacline. Surface ornament of fine rounded costellae, numbering about 22 in a 5-mm sector at 10-mm growth stage and increasing by branching and intercalation, crossed by fine concentric filae giving ribs a beaded appearance.

Pedicle valve interior with stout hinge teeth diverging at  $90^{\circ}-100^{\circ}$  and supported by reduced dental lamellae. Large, roundly triangular, flabellate muscle field about two-thirds as long as valve, bounded posteriorly by low ridges and bisected by low, slender median myophragm.

Brachial valve interior with prominent bilobed cardinal process situated on low notothyrial platform. Strong inner and outer socket ridges bound large oval sockets. Short anderidia and low median ridge extend anteriorly from notothyrial platform to bound anterior adductor muscle scars.

Dimensions (in mm)		
Pedicle valves	length	width
AM 5184	18.3	25.4
AM 5185	10.6	16.1
	9.2	13.4
AM 5186	13.7	21.6
	7.4	10.9
	14.4	19.8
	19.1	30.9
	7.2	11.4

#### Discussion

The specimens described herein are referable to Australostrophia because of their distinctive ornament and chonostrophiid-like cardinalia. Only three species are currently assigned to this genus, the type species Australostrophia mesembria (Clarke, 1913), the much smaller A. senegalensis Racheboeuf & Villeneuve, 1989, and A. clarkei Racheboeuf & Herrera, 1994. Of these the last most closely resembles the specimens described here. Indeed, they are virtually identical to specimens described from Bolivia by Isaacson (1977) and Racheboeuf & Branisa (1985) as A. mesembria but subsequently treated as a separate species by Racheboeuf & Herrera (1994).

The pedicle valve described and figured by Reed (1903) as *Stropheodonta* cf. S. concinna cannot be assigned to that species because it lacks the denticulate hinge line of *Protoleptostrophia* to which that species belongs. The specimen is better placed in A. clarkei, as it bears close resemblance to the specimens described here.

### Family Anopliidae Muir-Wood, 1962

### Genus Anoplia Hall & Clarke, 1892

Anoplia cf. A. belenensis Racheboeuf & Branisa, 1985

Fig. 6

Compare:

Anoplia belenensis Racheboeuf & Branisa, 1985: 1437, figs 7.1-7.7, table 5.

# Material and horizon

Twelve pedicle and 9 brachial valves from the Voorstehoek Formation near Uitenhage, eastern Cape Province (Fig. 2).

# Description

Small concavo-convex shells with transverse semicircular outline, maximum width at hinge line; cardinal extremities rounded. Pedicle valve about threequarters as long as wide; moderately convex in lateral profile, height about onethird of valve length. Umbo small; interarea short, flat, apsacline with small convex pseudodeltidium covering apical portion of delthyrium. Brachial valve gently concave with very short, flat, hypercline interarea. Shell exterior smooth.

Pedicle valve interior with small hinge teeth. Myophragm short, about onethird as long as valve. Muscle field well impressed, about as long as wide, bounded posteriorly by strong ridges diverging at about 80°. Diductor scars

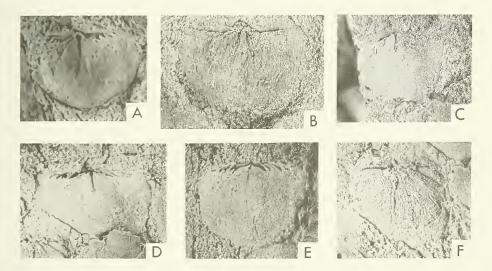


Fig. 6. Anoplia cf. A. belenensis Racheboeuf & Branisa, 1985. A. AM 5181, internal mould of a pedicle valve, × 3.8. B. AM 5180, external mould of a brachial valve, × 4. C. AM 5183, internal mould of a pedicle valve, × 4. D. AM 5182-2, internal mould of a pedicle valve, × 3.8. E. AM 5182-1, internal mould of a pedicle valve, × 4.8. F. AM 5182-3, external mould of a brachial valve, × 4.3. All from the Voorstehoek Formation near Uitenhage, eastern Cape.

elongate, triangular in outline with rounded anterior margins; diverging anteriorly. Adductor scars small, narrow. Roots of up to four spines observed along posterior margin on either side of beak.

Brachial valve interior poorly preserved. Cardinal process very small, bilobed. No median septum. One pair of accessory septa about one-half as long as valve, diverging anteriorly at 22°.

*Dimensions* (in mm)

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Pedicle valves	length	width
AM 5181	5.9	8.5
AM 5182	6.0	8.0
	<i>c</i> . 5	с. б
AM 5183	4.5	6.6

#### Discussion

The lack of radial ornament and absence of a dorsal median septum, but with a pair of diverging accessory septa, suggest placement in *Anoplia*. In size and shape, the specimens described here are very similar to those described from Bolivia by Racheboeuf & Branisa (1985), and they must be regarded as being closely related. However, more and better-preserved material is required before unequivocal assignment to the species is warranted. The specimens can be separated from the other Bolivian species, *A. mariae* Racheboeuf, 1992, which has two pairs of accessory septa in the dorsal valve and only two spines along the posterior margin.

These specimens represent the first record of the genus from South Africa.

Family Chonetidae Bronn, 1862 Subfamily Chonetinae Bronn, 1862 Genus *Aseptonetes* Isaacson, 1977

Aseptonetes capensis sp. nov. Fig. 7

*Chonetes* aff. *setiger* Hall: Reed, 1903: 174, pl. 21 (figs 4–5). *Chonetes* aff. *setiger* Hall: Reed, 1907: 170, 223. *Chonetes stübeli* non Ulrich. Reed, 1925: 44.

#### Material

*Holotype*. AM 5174 in the Albany Museum, Grahamstown. Internal and external moulds of joined pedicle and brachial valves from the Gydo Formation at Wuppertal (Fig. 2).

*Paratypes.* AM 5175-AM 5179, 19 brachial and 20 pedicle valves from the Gydo Formation at Wuppertal in the western Cape and three pedicle valves from the same formation in the Cockscomb area, south-east of Steytlerville in the eastern Cape. Further material is from the Voorstehoek Formation near

Uitenhage, eastern Cape (3 brachial and 14 pedicle valves) and from two localities within the Waboomberg Formation in the western Cape, including a pedicle valve from Tafelberg in the Ceres district, plus a pedicle and a brachial valve from the Hex River Valley, between Worcester and Touws River, both in the western Cape (Fig. 2).

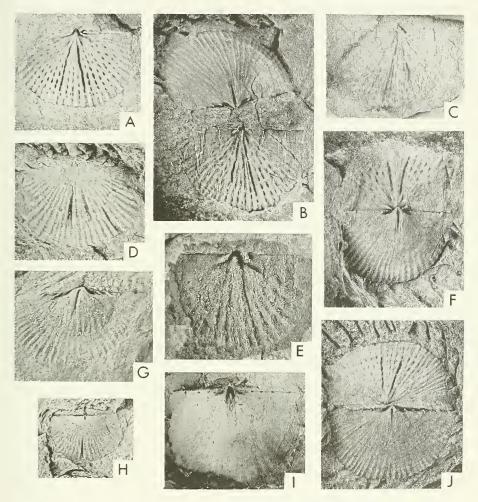


Fig. 7. Aseptonetes capensis sp. nov. A. AM 5174-1a, holotype, internal mould of a brachial valve,  $\times$  3.8. B. AM 5174-2, internal mould of a pedicle valve and a brachial valve,  $\times$  3.7. C. AM 5174-2, latex cast of brachial valve interior,  $\times$  3.8. D. AM 5175-2, external mould of a pedicle valve,  $\times$  5.3. E. AM 5178, internal mould of a brachial valve,  $\times$  5. F. AM 5174-3, internal mould of conjoined pedicle and brachial valves,  $\times$  4.8. G. AM 5179, internal mould of a pedicle valve,  $\times$  3. H. AM 5175-3, external mould of a brachial valve,  $\times$  5.1. I. AM 5177, latex cast of a pedicle valve interior,  $\times$  4.3. J. AM 5176, internal mould of conjoined pedicle and brachial valves,  $\times$  4.5. A-D, F and H-J come from the Gydo Formation at Wuppertal, western Cape; E and G come from the Voorstehoek Formation near Uitenhage, eastern Cape.

#### Diagnosis

Small chonetids with fairly coarse V-shaped ribs and lacking dorsal median septum. Anderidia and ventral median myophragm better developed than in the closely related *A. boucoti* Isaacson.

# Description

Small to medium concavo-convex shells with transversely subrectangular outline; maximum width along hinge line. Pedicle valve between two-thirds and three-quarters as long as wide; strongly and evenly convex in lateral profile but anterior profile with strongly convex median portion and more gently convex flanks. Ventral interarea curved orthocline to apsacline; delthyrium partially closed apically by convex triangular pseudodeltidium. Dorsal interarea flat, hypercline; chilidium strongly convex. Radial ornament of fairly coarse V-shaped costae and costellae increasing by bifurcation and intercalation to number 32-48 in shells between 5 mm and 11 mm long, with a density of 2-4 per millimetre at anterior margin. Four or five spines, seen as oblique openings on valve interiors, more or less symmetrically arranged on each side of umbo with the inner three being more closely spaced than the outer two.

Pedicle valve interior with stout, widely divergent, elongate hinge teeth supported by reduced dental lamellae. Muscle field not clearly defined but broadly triangular, flabellate, less than half as long as valve. Short median myophragm divides muscle field and extends for about one-third of valve length.

Brachial valve interior with well-developed, high, distally bilobed cardinal process and well-defined alveolus. Deep oval sockets bounded by strong, widely divergent inner socket ridges and less well-developed outer ones. Anderidia short, slender, diverging at an angle of about 35° and extending for about one-quarter of valve length. Median septum absent. Accessory septa originate anterior to alveolus, diverge at about 20° and extend for four-fifths of valve length.

#### Dimensions (in mm)

Pedicle valves	length	width
AM 5174	5.9	7.8
	4.2	6.2
AM 5175	5.0	6.6
AM 5176	4.6	7.9
AM 5177	6.5	9.4
AM 5179	7.2	11.0

#### Discussion

The small size, relatively coarse V-shaped radial ornament, and lack of median septum in the brachial valve suggest that these specimens belong in *Aseptonetes*. However, Racheboeuf & Branisa (1985) suggested that the specimens originally described by Isaacson (1977) were immature and did not show the adult characteristics. They described and figured somewhat larger shells that show a well-developed median septum but lack accessory septa. They stated that these specimens occurred on the same slabs as specimens bearing a close resemblance to Isaacson's type specimens and therefore represent later growth stages.

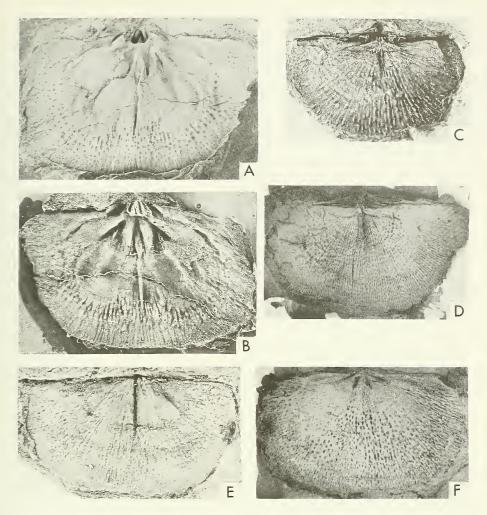


Fig. 8. Notiochonetes skottsbergi (Clarke, 1913). A-B. AM 4805, internal mould and latex cast of a brachial valve, × 1.5. C. AM 5192, external mould of a brachial valve, × 2.0. D. SAM-6713, latex cast of a brachial valve exterior, × 1.3.
E. SAM-3391, internal mould of a pedicle valve, × 1.9. F. AM 4808, latex cast of a brachial valve exterior, × 1.4. A, B, and F are from the Tra-Tra Formation, and C is from the Waboomberg Formation, all from north-east of Montagu, western Cape; D-E are from the Gydo Formation in the Ceres district, western Cape.

The Bokkeveld Group specimens described here overlap in size range with both Isaacson's (1977) and Racheboeuf & Branisa's (1985) specimens, but none are as large as their biggest shells. All bear a close resemblance to *A. boucoti* as described by Isaacson but none are similar to those described by Racheboeuf & Branisa. They also occur on the same pieces of rock as larger chonetids that do show the development of a median septum. However, there is no overlap in sizes, the larger shells have rounded rather than V-shaped ribs, and there are certainly no intermediate morphologies. The larger specimens are referable to *Pleurochonetes falklandicus* Morris & Sharpe but the smaller ones cannot be regarded as juveniles of this species.

To this author, *Aseptonetes* is a valid genus as defined by Isaacson (1977), and the larger specimens described and figured by Racheboeuf & Branisa probably should not be assigned to it. This being the case, then the subfamilial placing of the genus should revert to the Chonetinae as originally assigned by Isaacson.

As previously mentioned, the South African specimens are very similar to Isaacson's *A. boucoti* but they are rather more coarsely ribbed and their anderidia and ventral median myophragms are longer. They are thus placed in a separate species.

Subfamily Notiochonetinae Racheboeuf, 1992 Genus Notiochonetes Muir-Wood, 1962 Notiochonetes skottsbergi (Clarke, 1913) Figs 8-9

For synonymy see Hiller (1987: 1152).

Dimensions (in mm)

Pedicle valves	length	width
SAM-3391	17.2	29.0
AM 4806–2		=>
	21.7	34.4
AM 4806–3	25.4	38.5

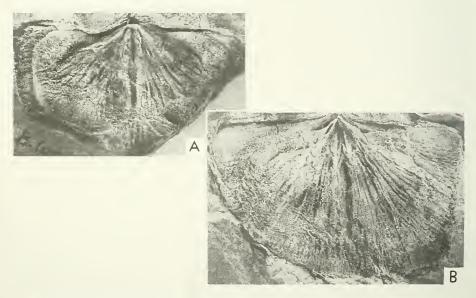


Fig. 9. Notiochonetes skottsbergi (Clarke, 1913). A. AM 4802-2, internal mould of a pedicle valve, × 1.7. B. AM 4806-3, internal mould of a pedicle valve, × 1.8. Both are from the Tra-Tra Formation north of Montagu, western Cape.

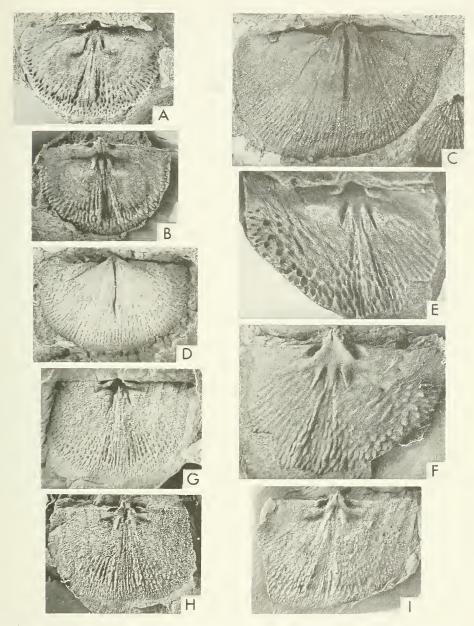


Fig. 10. Pleurochonetes falklandicus (Morris & Sharpe, 1846). A-B. AM 4811, internal mould and latex cast of a brachial valve, × 2. C. SAM-13399, internal mould of a pedicle valve, × 2.9. D. AM 4812, internal mould of a pedicle valve, × 2.2. E-F. SAM-13399, internal mould and latex cast of a brachial valve, × 3. G-H. AM 4802, internal mould and latex cast of a brachial valve, × 1.8. I. AM 4801, latex cast of a brachial valve interior, × 2. A, B and D are from the Gamka Formation in the Hex River Valley area of the western Cape; C-F are from the western Cape but locality and horizon are uncertain; G, H and I are from the Uitenhage district, eastern Cape (horizon is uncertain but probably the Gydo Formation).

# Remarks

This species was fully described by Hiller (1987) and nothing more is added here. It has been recorded from the Gydo and Voorstehoek formations in the Ceres district, the Voorstehoek Formation near Uitenhage, and the Tra-Tra Formation north-east of Montagu in the western Cape (Fig. 2).

#### Genus Pleurochonetes Isaacson, 1977

#### Pleurochonetes falklandicus (Morris & Sharpe, 1846)

Fig. 10

For synonymy see Hiller (1987: 1149).

Dimensions (in mm)

Pedicle valves	length	width
AM 4812	13.0	20.0
SAM-13399	12.3	18.0

# Remarks

This species was fully described by Hiller (1987) and nothing further is added here. It is well represented in widespread exposures of the Gydo, Gamka, and Voorstehoek formations, particularly in the western and southern Cape.

### CONCLUSIONS

This study expands the known diversity of chonetacean brachiopods in the South African Devonian and draws attention to the close similarity between the Bokkeveld Group fauna and the Malvinokaffric Realm faunas of Bolivia, Brazil, Argentina, Paraguay, Uruguay and Peru. Unfortunately, knowledge of chonetaceans in South American countries other than Bolivia and Argentina is incomplete, because of a lack of recent publications. Therefore, the significance of the apparent absence of genera such as *Austronoplia*, *Babinia* and *Eodevonaria* cannot be properly assessed at this stage. Certainly more work is required on the South African fauna, especially from those stratigraphic units that are under-represented in present collections. Only then will we be in a position to better understand Lower-Middle Devonian biogeography.

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#### REFERENCES

- BOUCOT, A. J. 1970. Practical taxonomy, zoogeography, paleoecology, paleogeography and stratigraphy for Silurian and Devonian brachiopods. *Proceedings of the North American Paleontological Convention*, Chicago, Part F: 566-611.
- Boucot, A. J. 1971. Malvinokaffric Devonian marine community distribution—and implications for Gondwana. *Anais da Academia brasileira de sciencias* **43** (Suplemento): 23-49.
- BOUCOT, A. J. 1975a. Evolution and extinction rate controls. Amsterdam: Elsevier.
- BOUCOT, A. J. 1975b. Reclassification of Australostrophia mesembria (Brachiopoda, Devonian). Journal of Paleontology 49: 633-637.
- BOUCOT, A. J. 1988. Devonian biogeography: an update. In: MCMILLAN, N. J., EMBRY, A. F. & GLASS, D. J. eds. Devonian of the World 3. Memoirs. Canadian Society of Petroleum Geologists 14: 211-227.
- BOUCOT, A. J., CASTER, K. E., IVES, D. & TALENT, J. A. 1963. Relationships of a new Lower Devonian Terebratuloid (Brachiopoda) from Antarctica. *Bulletin of American Paleontology* **46**: 81-151.
- BOUCOT, A. J. & HARPER, C. W. 1968. Silurian to Lower Middle Devonian Chonetacea. *Journal of Paleontology* **42**: 143–176.
- BOUCOT, A. J., JOHNSON, J. G. & DOUMANI, G. A. 1965. The Lower Devonian fauna of the Horlick Formation, Ohio Range, Antarctica. Articulate Brachiopoda. In: HADLEY, J. B. ed. Geology and paleontology of the Antarctic. Antarctic Research Series, Washington 6: 255-261.
- BOUCOT, A. J., JOHNSON, J. G. & TALENT, J. A. 1969. Early Devonian brachiopod zoogeography. Special Papers of the Geological Society of America **119**: 1–113.
- BRANISA, L. 1965. Los Fosiles Guias de Bolivia. Boletín Servicio geológico de Bolivia 6: 1-282.
- BRUNTON, C. H. C. 1972. The shell structure of chonetacean brachiopods and their ancestors. Bulletin of the British Museum (Natural History) (A, Geology) 21: 1-26.
- CLARKE, J. M. 1913. Fosseis devonianos do Paraná. Monografias do Serviço geológico e mineralógico do Brasil 1: 1-353.
- CLOUD, P. E. 1942. Terebratuloid Brachiopoda of the Silurian and Devonian. Special Papers of the Geological Society of America 38: 1-182.
- COOPER, M. R. 1986. Facies shifts, sea-level changes and event stratigraphy in the Devonian of South Africa. South African Journal of Science 82: 255-258.
- COPPER, P. 1977. Paleolatitudes in the Devonian of Brazil and the Frasnian-Famennian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **21**: 165–207.
- HERRERA, Z. A. 1991. Taxonomia, bioestratigrafía y paleobiogeografía de los braquiópodos de la Formación Talacasto (Devónico) de la Precordillera Argentina. Unpublished doctoral thesis, Universidad de Córdoba, Argentina.
- HILLER, N. 1987. The identity of *Chonetes falklandicus* (Brachiopoda, Devonian). *Journal* of *Paleontology* **61**: 1148–1155.
- HILLER, N. & DUNLEVEY, J. N. 1978. The Bokkeveld-Witteberg boundary in the Montagu-Touws River area, Cape Province. Transactions of the Geological Society of South Africa 81: 101-104.
- HILLER, N. & THERON, J. N. 1988. Benthic communities in the South African Devonian. In: MCMILLAN, N. J., EMBRY, A. F. & GLASS, D. J. eds. Devonian of the World 3. Memoirs. Canadian Society of Petroleum Geologists 14: 229-242.
- ISAACSON, P. E. 1977. Devonian stratigraphy and brachiopod paleontology of Bolivia. Part A: Orthida and Strophomenida. *Palaeontographica* (A) 155: 133–192.
- KNOD, R. 1908. Devonische Faunen Boliviens. In: STEINMANN, G. Beiträge zur Geologie und Paläontologie von Südamerika. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie (Beilagebände) 25: 493–600.
- KOZLOWSKI, R. 1913. Fossiles dévoniens du Brésil. Annales de paléontologie 8: 1-19.
- KOZLOWSKI, R. 1923. Faune dévonienne de Bolivie. Annales de paléontologie 12: 1-112.
- MELO, J. H. G. DE. 1988. The Malvinokaffric Realm in the Devonian of Brazil. In: MCMILLAN, N. J., EMBRY, A. F. & GLASS, D. J. eds. Devonian of the World 1. Memoirs. Canadian Society of Petroleum Geologists 14: 669-703.

- MORRIS, J. & SHARPE, D. 1846. Description of eight species of brachiopodous shells from the Palaeozoic rocks of the Falkland Islands. *Quarterly Journal of the Geological Society, London* 2: 274-478.
- MUIR-WOOD, H. M. 1962. On the morphology and classification of the brachiopod suborder Chonetoidea. London: Trustees of the British Museum (Natural History).
- RACHEBOEUF, P. R. 1990. Les Brachiopodes Chonetacés dans les assemblages benthiques siluriens et devoniens. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 81: 141-171.
- RACHEBOEUF, P. R. 1992. Los chonetáceos (Braquiópodos) del Devónico Boliviano: Bioestratigrafía y datos taxonómicos complementarios. *Revista española de Paleontologia* 7: 31-52.
- RACHEBOEUF, P. R. & BRANISA, L. 1985. New data on Silurian and Devonian chonetacean brachiopods from Bolivia. *Journal of Paleontology* **59**: 1426–1450.
- RACHEBOEUF, P. R. & HERRERA, Z. A. 1994. On some new Malvinokaffric Silurian and Devonian chonetacean brachiopods, and reclassification of others. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1994 (9): 541-560.
- RACHEBOEUF, P. R. & VILLENEUVE, M. 1989. Australostrophia senegalensis n. sp.: first chonostrophiid brachiopod (Chonetacea) from NW Africa. Implications for the northwestern Gondwanaland margin. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 1989 (12): 737-748.
- REED, F. R. C. 1903. Brachiopoda from the Bokkeveld Beds. Annals of the South African Museum 22: 165–200.
- REED, F. R. C. 1906. New fossils from the Bokkeveld Beds, South Africa. *Geological Magazine* 3: 301–310.
- REED, F. R. C. 1907. The fauna of the Bokkeveld Beds. *Geological Magazine* 4: 165-171, 222-232.
- REED, F. R. C. 1925. Revision of the fauna of the Bokkeveld Beds. Annals of the South African Museum 22: 27-225.
- SHARPE, D. 1856. Description of Palaeozoic Mollusca from South Africa. Transactions of the Geological Society, London (2) 7: 206-210.
- SOUTH AFRICAN COMMITTEE FOR STRATIGRAPHY. 1980. Stratigraphy of South Africa. Part 1. Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophuthatswana, Transkei and Venda. Handbook of the Geological Survey of South Africa 8: 1–690.
- TANKARD, A. J. & BARWIS, J. H. 1982. Wave-dominated deltaic sedimentation in the Devonian Bokkeveld basin of South Africa. *Journal of Sedimentary Petrology* 52: 959-974.
- TANKARD, A. J., JACKSON, M. P. A., ERIKSSON, K. A., HOBDAY, D. K., HUNTER, D. R. & MINTER, W. E. L. 1982. Crustal evolution of southern Africa—3.8 billion years of earth history. New York: Springer-Verlag.
- THERON, J. N. 1970. A stratigraphical study of the Bokkeveld Group (Series). In: HAUGHTON, S. H. ed. Proceedings and Papers of the Second International Gondwana Symposium: 197-204. Pretoria: Council for Scientific and Industrial Research.
  THERON, J. N. 1972. The stratigraphy and sedimentation of the Bokkeveld Group.
- THERON, J. N. 1972. The stratigraphy and sedimentation of the Bokkeveld Group. Unpublished doctoral thesis, University of Stellenbosch, South Africa.
- THOMAS, I. 1905. Neues Beiträge zur Kenntnis der devonischen Fauna Argentiniens. Zeitschrift der Deutschen geologischen Gesellschaft 57: 233-290.
- Toots, H. 1965. Orientation and distribution of fossils as environmental indicators. Guidebook. 19th Annual Field Conference, Wyoming Geological Association: 219-229.
- ULRICH, A. 1893. Palaeozoische Versteinerungen aus Bolivien. In: STEINMANN, G. Beiträge zur Geologie und Paläontologie von Südamerika. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie (Beilagebände) 8: 5-116.